

Origins of Mathematical Intuitions

The Case of Arithmetic

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Mathematicians frequently evoke their “intuition” when they are able to quickly and automatically solve a problem, with little introspection into their insight. Cognitive neuroscience research shows that mathematical intuition is a valid concept that can be studied in the laboratory in reduced paradigms, and that relates to the availability of “core knowledge” associated with evolutionarily ancient and specialized cerebral subsystems. As an illustration, I discuss the case of elementary arithmetic. Intuitions of numbers and their elementary transformations by addition and subtraction are present in all human cultures. They relate to a brain system, located in the intraparietal sulcus of both hemispheres, which extracts numerosity of sets and, in educated adults, maps back and forth between numerical symbols and the corresponding quantities. This system is available to animal species and to preverbal human infants. Its neuronal organization is increasingly being uncovered, leading to a precise mathematical theory of how we perform tasks of number comparison or number naming. The next challenge will be to understand how education changes our core intuitions of number.

Key words: number; neuroimaging; mathematics

What then is mathematics if it is not a unique, rigorous, logical structure? It is a series of great intuitions carefully sifted, and organized by the logic men are willing and able to apply at any time.

—Morris Kline, *Mathematics: The Loss of Certainty* (p. 312)

Introduction

All great mathematicians appeal to their “intuition.” One of the most famous proponents of this concept was the French mathematician Jacques Hadamard, who published a systematic inquiry into his fellow mathematicians’ practices (Hadamard 1945). Hadamard reported that many major mathematical dis-

coveries were preceded by long periods of unconscious “incubation” followed by sudden insight. He also quoted Einstein’s well-known introspection: “Words and language, whether spoken or written, do not seem to play any role in my thinking mechanisms. The mental entities that serve as elements of my thought are certain signs or images, more or less clear, that can ‘at will’ be reproduced or combined.” Henri Poincaré saw intuition as the foundation upon which the mathematical enterprise was based. Davis and Hersh, in their description of “the mathematical experience,” went even further (and probably too far) by viewing intuition as the single faculty that allows us to do mathematics: “In the realm of ideas, of mental objects, those ideas whose properties are reproducible are called mathematical objects, and the study of mental objects with reproducible properties is called mathematics. Intuition is the faculty by which we can consider or examine

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these (internal mental) objects” (Davis, Hersh, & Marchisotto 1995, p. 399).

The problem with these statements is that they fail to define what an intuition is. Indeed, the concept, like many other theoretical constructs of folk psychological origin (“attention,” “association,” “consciousness,” and others) remains suspect in present-day cognitive neuroscience because it is unclear whether it corresponds to a well-characterized mental entity or process. I would like to argue, however, that recent research in numerical cognition fleshes out the concept of intuition, at least within the small domain of elementary arithmetic. The results indicate that a sense of number is part of *Homo sapiens*’ core knowledge, present early on in infancy, and with a reproducible cerebral substrate. It permits a rapid evaluation of (1) approximately how many objects are present in a scene, (2) whether this number is more or less than another number, and (3) how this number is changed by simple operations of addition and subtraction. Its operation obeys three criteria that may be seen as definitional of the term “intuition”: it is fast, automatic, and inaccessible to introspection. These properties, far from implying that this intuition is inaccessible to scientific understanding, constitute a decipherable signature of intuition, and we shall see that a simple but precise quantitative mathematical model can be proposed for some of the simplest aspects of their operation.

It will be important, in the following, to clearly distinguish symbolic and nonsymbolic aspects of elementary arithmetic. Symbolic arithmetic deals with how we understand and manipulate numerals and number words such as “five” or “twenty.” Nonsymbolic arithmetic is concerned with how we grasp and combine the approximate cardinality or “numerosity” of concrete sets of objects (such as visual dots, sounds, and actions). Our core knowledge of arithmetic is essentially nonsymbolic—the availability of number symbols varies across cultures and arises late in human development. Nevertheless, number symbols, once available, become strongly attached to the corresponding

nonsymbolic representations of numbers and, thereafter, a form of “second-order intuition” seems to develop, as the links between symbols and quantities themselves become fast, automatic, and unconscious. In the second part of this chapter, we shall review current evidence concerning this symbol grounding problem.

Arithmetic Intuition: A Cross-Cultural Universal

A recently discovered effect of numerical adaptation (Burr & Ross 2008) provides an excellent introduction to nonsymbolic numerical intuition. Stare at the fixation point in Figure 1, which has 10 dots at left and 100 dots at right. Then after 30 sec of adaptation, shift to Figure 2. You should have the strong impression that the left display is more numerous than the right one, although both have exactly 40 dots. You may also have the erroneous impression that there are much less than 40 dots in both cases (see Izard & Dehaene 2008). Both adaptation and underestimation effects have been found to resist extensive manipulation of the non-numerical parameters of the display, thus evading simple explanations in terms of size, density, or contrast.

At the moment of this writing, why adaptation can have such a profound effect on numerosity estimates remains largely unexplained. Yet the fact that numerical percepts impose themselves upon us so immediately, automatically, and without conscious control (even if we know that the numbers are equal) points to the operation of a special and largely automatic processing system. As noted by Burr and colleagues, “Just as we have a direct visual sense of the reddishness of half a dozen ripe cherries, so we do of their sixishness.”

Cross-cultural research suggests that this ability is present in humans without mathematical training. Although number words figure among the most frequent lexical items and are present in many languages, it is still possible to find aboriginal, Amazonian or African

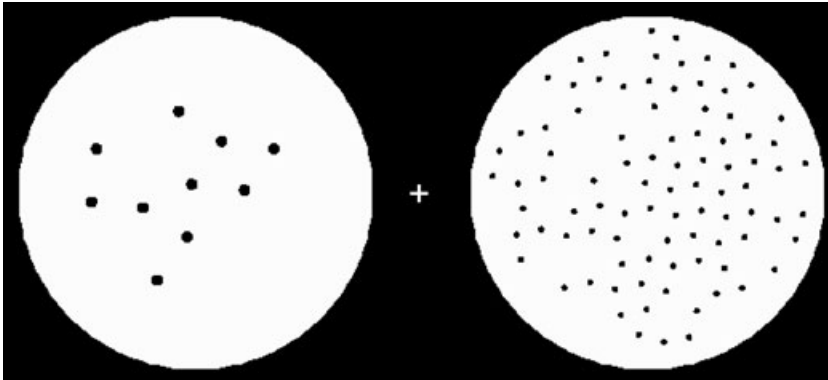


Figure 1. Numerosity adaptation. Stare at the fixation cross for 30 sec, then see Figure 2.

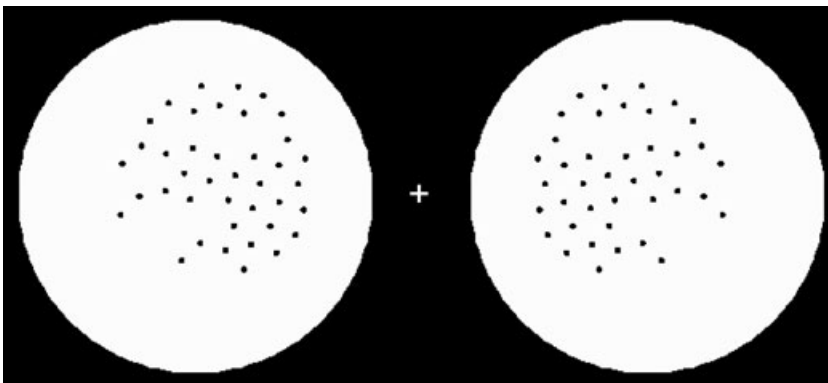


Figure 2. Numerosity adaptation. After staring at Figure 1 for 30 sec, you should experience the strong impression that the left display is more numerous than the right, although they are actually identical (after Burr & Ross 2008).

cultures with a reduced lexicon for number, sometimes as limited as to include only words for “one,” “two,” and “many.” In spite of this linguistic limitation, and of their frequent lack of access to education, these people exhibit a remarkable nonverbal competence for elementary arithmetic—keeping in mind that their knowledge is approximate rather than exact. Peter Gordon (2004) observed how the Pirahã, whose lexicon stops at two, could approximately match two numerosities. They could not perform an exact match, however (apparently not even with the smallest numbers, 1 and 2), leading Gordon to claim that their numerical cognition was “incommensurate” with ours. This terminology appears misleading, however, because on average their matching responses

were almost perfectly linearly correlated with the true numerosity—with a standard deviation that also increased in direct proportion to the inferred numerosity.

Pierre Pica, Véronique Izard, Cathy Lemer, and I studied the Mundurucu, another Amazonian group that has number words up to five (Pica, Lemer, Izard, & Dehaene 2004). We discovered that Mundurucu adults and even children possess an excellent capacity to discriminate two sets based on their number, decide which is more numerous, or even approximately add or subtract two such numerosities—even with numerosities up into the 50s and more, way beyond their naming range. Their psychophysical behavior was qualitatively similar to that of Western students: both were

determined by Weber's law, which states that the minimal difference between two numbers that leads to a fixed level of discrimination varies in direct proportion to the size of the numbers. Weber's law has been observed with a great variety of perceptual continua such as pitch, loudness, or brightness. Its observation in the number domain further strengthens the hypothesis that arithmetical intuition starts within a basic perceptual system for estimating approximate number. Obviously, then, intuitions concerning the cardinality of sets are available to isolated adults, even in the absence of formal education and a sophisticated mathematical language.

Recently, Brian Butterworth and his colleagues extended this cross-cultural research to a group of 4- to 7-year-old indigenous Australian children (Butterworth, Reeve, Reynolds, et al. 2008). Using one-to-one matching tasks similar to Gordon's, but extended to include cross-modal addition and sharing conditions, they observed a high level of performance that was indistinguishable from that of English-speaking children. Somewhat controversially, they concluded that concepts of exact number are already available to both groups, regardless of language. The data, however, indicate only approximate performance, subject to Weber's law, with a rather sharp drop for numbers above three, suggesting a contribution from both estimation and subitizing (Butterworth et al. 2008, Figs. 3 and 4). It is true that cross-modal matching performance remained relatively high even with numbers 5 and above, but in the absence of more knowledge about the children's education and the availability of finger or body pointing symbols in this culture, it is hard to reach a firm conclusion as to whether the results reflected a genuine grasp of exact number in the absence of education, especially given that the matching task lends itself to a variety of spatial cueing strategies. Uncontroversially, however, all cross-cultural studies point to the fact that approximate number is an intuition available to humans regardless of language and education.

Intuitions of Numbers in Infancy and Early Childhood

Piaget's influential research, summarized in *The Child's Conception of Number* (1952), initially suggested that young children do not have any stable, invariant representation of number, and that knowledge of arithmetic emerges slowly as a logical construction. Less than 30 years later, Rochel Gelman and Randy Gallistel's work, summarized in *The Child's Understanding of Number* (1978), played an instrumental role in overturning the Piagetian view. Gelman and Gallistel showed that even preschoolers had intuitions in arithmetic, since they could detect unexpected changes in small numerosities (the "magic" experiments) or violations in the counting routine. From this point, it was only a small leap to ask whether infants also have a sense of number (Starkey & Cooper 1980). Today, a large set of behavioral studies using habituation and violation-of-expectancy paradigms has revealed a clear sensitivity to large numbers in 4- to 6-month-old infants. For instance, infants discriminate when the numerosity of a set unexpectedly changes from 8 to 16 dots or vice-versa, even when non-numerical parameters such as density and total surface are tightly controlled (Xu & Spelke 2000). Infants also detect violations of approximate addition and subtraction events. For instance, upon seeing five objects being hidden behind a screen, then another five objects being added, they appear to expect 10 objects and express a form of surprise through longer looking times when the screen collapses and only five objects are revealed (McCrink & Wynn 2004; Wynn 1992a).

In the range of small numbers one, two, and three, the issue of numerical competence in infancy has been subject to much more debate. Initial observations suggested numerical discrimination in infants and even in newborns (Antell & Keating 1983; Bijeljic-Babic, Bertoini, & Mehler 1991). Further studies with tighter controls for non-numerical parameters, however, failed to replicate these findings and suggested that performance was driven by

low-level confounds such as the total amount of stuff (Feigenson, Dehaene, & Spelke 2004; Mix, Levine, & Huttenlocher 1997; Simon 1999; Xu & Spelke 2000). A resolution of this debate now seems to be in sight. The newer results indicate that infants can attend to either numerical or non-numerical parameters, and do so to a variable extent depending on the experimental design and, particularly, on the variability of these parameters in the stimulus set. For instance, Feigenson (2005) demonstrated that infants attend to visual numerosity, even in the range from one to three objects, as long as the sets comprise highly distinctive objects rather than identical replicas of the same object. Extensive recent work by Sara Cordes and collaborators now suggests that number is indeed available to infants, even in the presence of variability in other cues. Cordes and Brannon (2008) go as far as to suggest that, for infants, using number is easier than using continuous extent, in the sense that a smaller proportional amount of change is required for infants to detect changes in the former than in the latter. A recent study using event-related potentials, to be further detailed below, also indicates discrimination of numbers 2 versus 3 in the absence of non-numerical confounds (Izard, Dehaene-Lambertz, & Dehaene 2008).

To what extent are these demonstrations of numerosity discrimination actually relevant to subsequent mathematical intuitions? Although it has long been proposed that infants' numerical discrimination abilities provide a foundation on which children base their subsequent understanding of the number domain (Dehaene 1997), until recently there was little direct empirical support for this suggestion. Recently, however, a behavioral study in preschoolers demonstrated that early arithmetic intuitions are translated into higher-than-chance performance in school-relevant symbolic arithmetic problems (Gilmore, McCarthy, & Spelke 2007). Gilmore, McCarthy, and Spelke gave 5- and 6-year-olds problems such as "Sarah has 21 candies, she gets 30 more, John has 34 candies—who has more?" The problems were simultane-

ously presented both orally, as spoken numerals, and in writing as Arabic numerals. However, note that the participants were preschoolers and had therefore received no training with numbers of that size, nor with the concepts of addition or subtraction. Nevertheless, they spontaneously performed much better than chance (60%–75%), regardless of their socioeconomic origins. Performance was approximate and depended on the ratio of the two numbers, again a clear signature of Weber's law. Importantly, variability in performance was predictive of achievement in the school's curriculum.

Similarly, Holloway and Ansari (2008) recently reported, in slightly older children aged from 6 to 8 years, that the variability in the distance effect during number comparison is predictive of mathematics achievement, but not of reading achievement. Finally, Halberda et al. (2008) showed a tight correlation between performance in nonsymbolic number comparison and achievement scores in mathematics (but not other domains) throughout the school curriculum. Altogether, and although a direct causal influence has not yet been demonstrated, those results suggest that a grasp of approximate numerosity and of distance relations between numbers, grounded in Weber's law, may govern the subsequent understanding of symbolic arithmetic.

The emphasis on the presence of early intuitions in young children should not be confused with a naïve nativist view of numerical development, according to which the foundations of arithmetic would all be present shortly after the birth. Clear limits on intuitions of arithmetic are evident around 2.5 to 4 years of age, when children begin to acquire number words. For a long period, children may know the meaning of the word *one* (for instance showing an ability to provide just one object or to name a set of numerosity one), but not the meaning of other numbers *two*, *three*, and above (for instance grabbing a random number of objects when asked to provide two) (Wynn 1992). Children slowly learn to map number words *one*, *two*, *three*, and

four to their corresponding quantities one by one, until suddenly they understand that each word maps onto a different number. It may take them at least another 6 months before they understand that larger number words such as “six,” “eight,” and “ten” map onto distinct quantities, and begin to grasp their order relations (Le Corre & Carey 2007). It is not until the age of five that they understand that a word such as “eight,” if it applies to a set, continues to apply after the objects are shuffled but ceases to apply if the set is increased by one, doubled, or halved (Condry & Spelke 2008; Lipton & Spelke 2006; Sarnecka & Gelman 2004).

Exactly how children eventually acquire higher-level intuitions of exact arithmetic remains a matter of intense theoretical debate (for specific proposals, see Gelman & Butterworth 2005; Le Corre & Carey 2007; Nunez & Lakoff 2000; Rips, Bloomfield, & Asmuth 2008; Spelke 2003). The intensity of this discussion is inversely proportional to the quality of the data: in truth, we know next to nothing about the psychological or neural structures that underlie our understanding of the basic principles of formal arithmetic such as successor function, commutativity, infinity, or induction. At the end of this review, we will briefly consider a tentative proposal for how the acquisition of exact number concepts (e.g., exactly six) is encoded at the neural level. For present purposes, however, we focus on the consensus area, which is that preschoolers and even infants, tested with nonsymbolic displays of numerosity, exhibit excellent performance even in subtle tests of comparison, addition, and subtraction (Barth et al. 2006). This early ability points to a particular cerebral substrate, to which we now turn.

Cerebral Networks of Number Sense

Calculation and the Intraparietal Area

The first imaging studies of calculation, using single photon emission computerized tomogra-

phy (SPECT), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI), quickly pointed to a remarkable fact: whenever adults calculate, a reproducible bilateral parietal activation is observed (Appolonio et al. 1994; Dehaene et al. 1996; Roland & Friberg 1985). The use of single-subject fMRI demonstrated that, although interindividual variability is somewhat larger than in studies of reading or face perception, the horizontal segment of the intraparietal sulcus (hIPS) is always consistently activated whenever adults compute simple comparison, addition, subtraction, or multiplication with Arabic numerals (Chochon, Cohen, van de Moortele, et al. 1999). Figure 3 shows the location of this region relative to other landmark areas of the human parietal lobe.

Initial studies probed the exact nature of the contribution of this region to the processing of numbers presented as Arabic numerals or as number words. Intraparietal activation was observed during a great variety of number-related tasks, including calculation but also larger–smaller comparison (Pinel, Dehaene, Riviere, et al. 2001) or even the mere detection of a digit among colors and letters (Eger, Sterzer, Russ, et al. 2003). The intraparietal region seems to be associated with an abstract, amodal representation of numbers inasmuch as it can be activated by numbers presented in various culturally learned symbolic notations such as Arabic numerals and spelled-out or spoken number words (Eger et al. 2003). Similar results have been consistently observed in experiments with adults from various countries and cultures including France, UK, USA, Austria, Singapore, China, and Japan. In a direct comparison of Chinese and English speakers, Tang et al. (2006) observed intraparietal activation at a similar location in the IPS during calculation and comparison tasks. They did however observe cultural variation in other surrounding areas, particularly in left premotor cortex (more active in Chinese subjects) and left perisylvian areas (more active in English subjects).

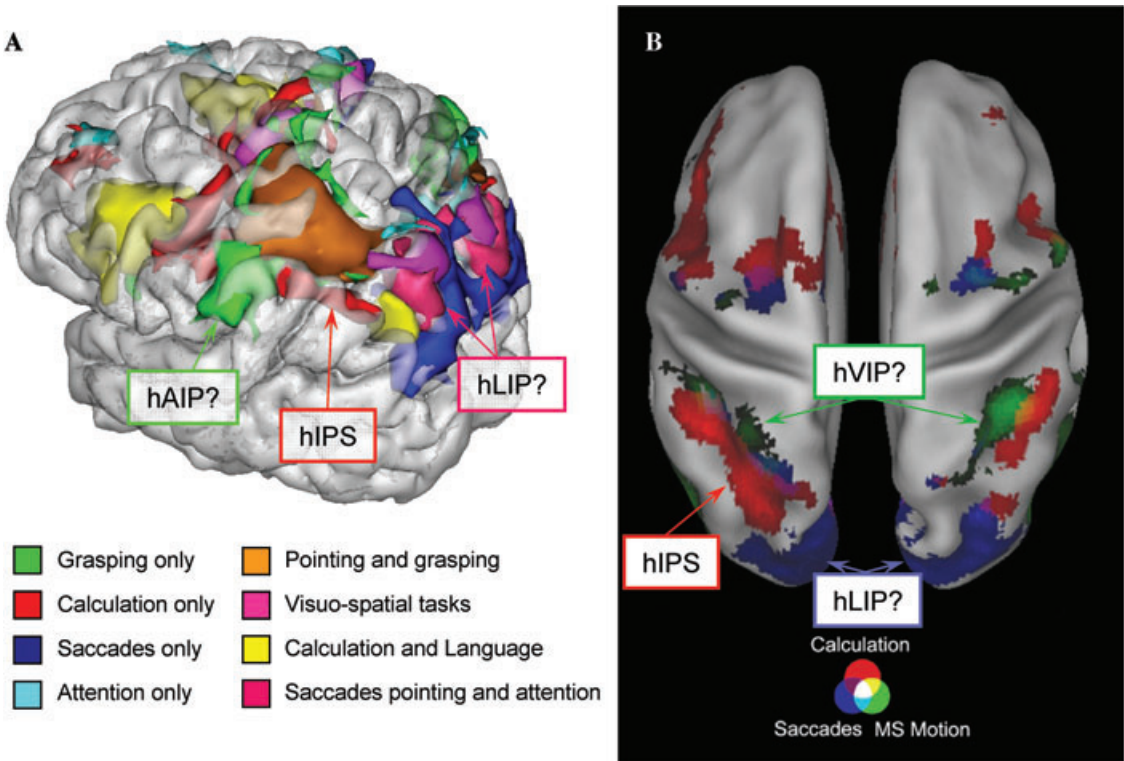


Figure 3. Anatomical and functional organization of human parietal lobe areas. **(A)** Activations reported in a study of six parietal functions in the same subjects (calculation, language, saccades, attention, pointing, and grasping tasks) (for details, see Simon et al., 2004; Simon et al., 2002). Calculation activates the horizontal segment of the intraparietal sulcus (hIPS, shown in red). In all subjects, the hIPS lies posterior to an area activated by grasping movements, thought to be a plausible human homolog of monkey anterior intraparietal area AIP (hAIP, shown in green). The hIPS is also anterior to a set of areas activated by saccadic eye movements (shown in blue, pink, and purple), one of which might be the human homolog of monkey lateral intraparietal area (hLIP). **(B)** Finer-grained study of the relationship between calculation, saccades, and multisensory motion in humans (Hubbard, Pinel, Jobert, et al. 2008). In macaque monkeys, tactile facial motion, and visual flow fields activate neurons in the ventral intraparietal area (VIP), where neurons tuned to number are also found. The same stimuli identify a plausible human homolog of VIP (hVIP), which overlaps partially with the hIPS activation observed during symbolic calculation, but is consistently mesial to it.

Linguistic and Nonlinguistic Networks for Arithmetic

It is likely that some of these additional, extraparietal activations relate to spoken or written language networks that are thought to supplement the core intraparietal system in order to perform exact symbol-based calculations or to retrieve arithmetic facts from linguistic memory. fMRI studies have indeed demonstrated that the intraparietal sulcus is most activated during tasks that call upon quantity manipulations, particularly approximation of addi-

tions or subtractions, whereas another set of areas involving the left angular gyrus and/or surrounding perisylvian cortices shows greater activation during operations of exact calculation that depend on explicit education and often rely on language-specific rote memorizing (Dehaene, Spelke, Pinel, et al. 1999; Lee 2000; Venkatraman, Siong, Chee, & Ansari 2006; Zago et al. 2008). During training with a given set of arithmetic facts, activation progressively shifts from the intraparietal region to the angular gyrus as subjects commit these facts to verbal memory (Delazer et al. 2003; Ischebeck

et al. 2006). Altogether, therefore, those results mesh well with the notion of a core system of number, associated with the bilateral intraparietal cortex and invariable across culture and education, and a distinct perisylvian circuit associated with language- and education-specific strategies for storing and retrieving arithmetic facts (Dehaene & Cohen 1995). Double dissociations following brain lesions further support this basic distinction: focal intraparietal lesions can cause drastic impairments in number sense, often affecting operations as simple as addition, subtraction, comparison or numerosity estimation, while lesions to perisylvian cortices or left basal ganglia generally impact on rote operations such as the multiplication table (Cipolotti, Butterworth, & Denes 1991; Lee 2000; Lemer, Dehaene, Spelke, et al. 2003).

Instrumental in characterizing the role of the intraparietal sulcus in core number sense have been neuroimaging studies that relied on nonsymbolic presentations of number as sets of dots or as series of tones (Castelli, Glaser, & Butterworth 2006; Piazza, Izard, Pinel, et al. 2004; Piazza, Mechelli, Price, et al. 2006; Piazza, Pinel, Le Bihan, et al. 2007). Attending to the numerosity of such stimuli suffices to induce a strong bilateral activation of the IPS (Castelli et al. 2006; Piazza et al. 2006). Even passively looking at a set of dots suffices to encode its numerosity and adapt to it, so that the intraparietal sulcus later shows a rebound fMRI response when the number is changed by a sufficient amount (Piazza et al. 2004). This fMRI adaptation method has also been used to demonstrate a convergence of symbolic and nonsymbolic presentations of numbers toward a common representation of quantity in the IPS (Piazza et al. 2007).

Early Parietal Response to Number in Infancy

When in development does the parietal cortex first begin to respond to number? fMRI and event-related potentials (ERPs) have shown that number-related parietal activations, par-

ticularly in the right hemisphere, are already present in 4-year-old children as they attend to the numerosity of sets (Cantlon, Brannon, Carter, et al. 2006; Temple & Posner 1998). Thus, the parietal mechanism of numerosity extraction seems to be already functional prior to arithmetic education in humans. As noted above, behavioral studies of numerical discrimination imply the presence of a functional numerosity processing system at an even earlier age, during infancy. Indeed, Berger et al. (2006) measured ERPs in 7-month-old infants as they viewed short movies depicting correct and incorrect nonsymbolic arithmetic operations ($1 + 1 = 2$ vs. $1 + 1 = 1$). The detection of these arithmetic violations was accompanied by a clear negativity recorded over anterior electrodes. This reaction was similar to the classical error-related negativity, thought to arise from the anterior cingulate cortex, which indexes error detection and correction. Presumably thus, this experiment reflected numerical competence only indirectly, without directly pinpointing to the cortical origins of this competence.

To visualize more directly the brain's responses to number in infants, we recorded event-related potentials from 3-month-old infants, while they were presented with a continuous stream of sets of objects (Izard et al. 2008). Within a given run, most sets had the same numerosity and were made of the same objects (e.g., repeatedly presented various images of three ducks). However, occasionally a test image would appear that could differ from the habituation images in either number, object identity, or both. Across different groups of subjects, the numbers involved ranged from 2 versus 3 to 4 versus 8 or 4 versus 12. In all cases, event-related potentials revealed that the infants' brain detected the two types of changes (number vs. object), yet with different underlying circuitry. Source reconstruction, using an accurate model of the infant's cortical folds, suggested that the right parietal cortex responded to numerical novelty, while the left occipitotemporal cortex responded to object

novelty. This ventral/dorsal double dissociation is similar to what has been observed in adults and 4-year-olds (Cantlon et al. 2006; Piazza et al. 2004): fMRI adaptation shows that the fusiform gyrus reacts to changes in object identity but not in number, and while the parietal regions react to changes in number but not in object identity. Thus, the results suggest that the well-known ventral–dorsal dissociation between object identity (“what”), versus object location, size, and motor affordance (“where” and “how”) (Goodale & Milner 1992) may already be in place at 4 months of age, and that number belongs to the parameters that are quickly extracted by the dorsal parietal pathway even in infants.

Specificity of the Intraparietal Region

An important and only partially resolved issue concerns whether any part of the intraparietal is uniquely specialized for number. In the present state of knowledge, the answer is a nuanced one. The intraparietal sulcus clearly contains a specialized subsystem for number in the sense that its activation during calculation cannot be reduced to simpler sensorimotor functions such as attention or response planning. However, there does not seem to be a single, isolated piece of cortex that responds solely to number—parameters of object size and location also seem to be coded by intermingled neuronal circuits distributed within the same general area of IPS.

As far as the first point is concerned, the parietal activation putatively associated with core “number sense” occupies a fixed location relative to other parietal areas involved in sensory, motor, and attentional functions (see Fig. 3). Our group used fMRI to study the cerebral organization of six different functions previously associated with parietal systems: finger pointing, manual grasping, visual attention orienting, eye movement, written word processing, and calculation (Simon et al. 2004; Simon, Mangin, Cohen, et al. 2002). All subjects showed a reproducible geometrical

layout of activations associated with these functions. Most notably, activation uniquely evoked by calculation was observed in the depth of the intraparietal sulcus and was surrounded by a systematic front-to-back arrangement of activation associated with grasping, pointing, attention, eye movement, and language-related activations. The systematicity of this organization was confirmed by subsequent research using more selective experiments specifically designed to isolate grasping, saccade, and attention-related functions (for review, see Culham, Cavina-Pratesi, & Singhal 2006).

As concerns the second point, several studies have now contrasted intraparietal activations during judgments of number versus other continuous dimensions such as physical size, location, angle, and luminance (Cohen Kadosh & Henik 2006; Cohen Kadosh et al. 2005; Fias, Lammertyn, Reynvoet, et al. 2003; Kaufmann et al. 2005; Pinel, Piazza, Le Bihan, et al. 2004; Zago et al. 2008). The results indicate that IPS activations do not cluster neatly into distinct regions specific for a given quantitative parameter. Rather, the activations show considerable overlap. This overlap is particularly strong for number and location (Zago et al. 2008) and for number and size (Kaufmann et al. 2005; Pinel et al. 2004), although a partial subspecialization for number processing is occasionally reported (Cohen Kadosh et al. 2005). There is also considerable overlap between the activations induced number and letter comparisons (Fias, Lammertyn, Caessens, et al. 2007).

Two interpretations of these overlapping activations have been proposed. Several authors have proposed that the intraparietal sulcus activation during arithmetic reflects a general function that is not specific to numbers (Fias et al. 2007; Shuman & Kanwisher 2004; Walsh 2003). Vincent Walsh, for instance, proposes that the parietal lobe contributes to a “generalized magnitude system,” which encompasses representations of space, time, and number. Alternatively, and while not denying that magnitude manipulation and transformation may be an overarching function of parietal-lobe

areas, my colleagues and I have proposed that the overlapping activation need not reflect a lack of neural specialization. Rather, analog quantities such as number, location, size, luminance, or time may well be coded by neuronal assemblies that are specialized, yet intermixed within the same voxels (Pinel et al. 2004). Under this interpretation, it may be wrong to generalize to parietal cortex the model of extreme specialization and discrete “modules” with sharp boundaries that emerged from studies of the fusiform face responses (Kanwisher, McDermott, & Chun 1997; Tsao, Freiwald, Tootell, et al. 2006). Rather, neuronal populations coding for number would be highly distributed in the intraparietal sulcus and would be intertwined and overlapping with representations of other quantitative parameters. Although the specialization debate is still far from being settled, as we shall now see, recent monkey neurophysiology nicely supports the concept of overlapping but specialized neural populations (Tudusciuc & Nieder 2007, see below).

Neural Codes for Number in the Macaque Monkey

Intraparietal Neurons Tuned to Numerosity

Human neuroimaging studies predicted that if a precursor of human numerical abilities existed in monkeys it might lie in the depth of the intraparietal sulcus, anterior to regions involved in memorized eye movements (plausibly relating to monkey lateral intraparietal area LIP) and posterior to regions involved in grasping objects (plausibly relating to monkey anterior intraparietal area AIP) (Simon et al. 2002, see Fig. 3). Indeed, in the same year, two independent groups of electrophysiologists working in the awake macaque monkey identified number-coding neurons within and near the intraparietal sulcus (Nieder, Freedman, & Miller 2002; Nieder & Miller 2004; Sawamura, Shima, & Tanji 2002). Although similar neurons were also found in the prefrontal cor-

tex, PFC neurons responded with a longer latency and showed greater delay-related activity, suggesting that the parietal neurons constitute a primary numerosity code, which prefrontal neurons held on-line during the delayed match-to-sample task.

The monkey intraparietal neural code for numerosity may be the evolutionary precursor onto which the human invention of arithmetic encroached. First, the analogy in cerebral location is striking. Numerosity-tuned neurons are mostly found in the depth of the intraparietal sulcus and often show visual flow-field responses, compatible with a location in ventral intraparietal area VIP (Tudusciuc & Nieder 2007). Likewise, human fMRI studies have located a plausible homolog of area VIP (Bremmer et al. 2001; Sereno & Huang 2006) at a location close to and overlapping with that of number-related responses (see Hubbard, Piazza, Pinel, et al. 2005). Recently our group further attempted to clarify the homologies between numerical processing regions and macaque areas LIP and VIP (Hubbard et al., submitted). To explore this question, we used physiologically inspired localizer tasks of saccadic eye movement, visual flow fields, and tactile face stimulation to identify plausible human homologs of LIP and VIP (see Fig. 3). We then examined the topographical relations between these activations and calculation-related activations. We also measured voxel-by-voxel correlations between these spots of activation. The results indicate that the hIPS activation during symbolic calculation overlaps partially with the human homolog of area VIP (though it is generally more lateral), suggesting a partial homology between human and macaque parietal regions (see Fig. 3).

The profile of response of these neurons also fits with the code for numerosity inferred from human studies. The neurons studied by Nieder and Miller are tuned to a particular numerosity (Nieder & Merten 2007; Nieder & Miller 2003, 2004). For instance it is possible to find some neurons that show a peak of firing for numerosity 1, another set for numerosity 2,

3, . . . all the way to numbers in the 30s. Furthermore, the tuning curves of these neurons show Gaussian variability on a log scale. For instance, neurons that show a firing peak when four objects are present also respond to three or five objects, and much less to one or to 10 objects. Collectively, these neurons form a distributed representation subject to Weber's law: each number is not coded in an exact manner, but only approximately and with an imprecision that increases linearly with number. The log-Gaussian neural code that was identified by Nieder and Miller in the macaque monkey is identical to the representation thought to underlie numerical judgments in human subjects, as derived either from behavioral research, as mentioned earlier, or from fMRI adaptation studies (Piazza et al. 2004, 2007).

Recent studies from Andreas Nieder's laboratory have further clarified the extent to which this code is abstract and specific to the number domain. Initially studies used only visual sets of simultaneously presented objects, but recent research has shown that, in some neurons at least, the code is abstract enough to respond to both sequential and simultaneous presentations of number (Nieder, Diester, & Tudusciuc 2006). Furthermore, at this single-neuron level, the code appears to be specific for number. Number neurons maintain their numerical selectivity in the face of considerable variation in the size, location, and nature of the objects in the set (Nieder et al. 2002). Conversely, distinct populations of neurons code for line length (Tudusciuc & Nieder 2007). These two types of neurons are intermingled within the same areas of the IPS, and can sometimes be recorded under the same electrode tip. Again, this distributed overlapping organization of multiple neural codes for quantitative dimensions is very similar to that inferred from human fMRI (Pinel et al. 2004).

Multiple Codes for Number

Recently, Roitman et al. (2007) uncovered another type of neural code for numerosity in

area LIP. Neurons in LIP behave differently from the IPS neurons discovered by Nieder and Miller in several respects. First, LIP neurons are not tuned to number. Rather, their firing rate varies monotonically with numerosity, either increasing or decreasing sharply with the logarithm of the number of objects in the neuron's receptive field. Second, these neurons have limited receptive fields and thus respond solely to the local numerosity within a certain retinotopic area, not to the total numerosity across the whole visual field.

Why would two quite distinct codes—monotonic versus tuned cells—coexist in the same individual? One possibility is that the monotonic cells are needed in order to compute the tuned-cell representation, so that monotonic and tuned codes would constitute two distinct stages in the computation of an invariant numerical representation. Jean-Pierre Changeux and I have presented a theoretical model of how numerosity can be extracted from visual displays (Dehaene & Changeux 1993), later elaborated by others (Verguts & Fias 2004; Verguts, Fias, & Stevens 2005). Our model illustrates how approximate numerosity can be extracted from a retinotopic map through three successive stages: (1) retinotopic coding of object locations regardless of object identity and size, thus yielding a normalized, constant amount of activation for each object; (2) summing of the activation on the object location map, thus yielding a representation of approximate numerosity by accumulation neurons; (3) thresholding of the activation in accumulation neurons by neurons with increasingly higher thresholds, yielding a bank of numerosity detector neurons each tuned to a specific numerosity. With only small modifications, the accumulation neurons may be identified with the LIP monotonic cells, and the numerosity detector cells with the VIP tuned cells. Anatomically, indeed, LIP neurons project directly to VIP. Furthermore, LIP number neurons have receptive fields, whereas VIP number neurons seem to respond to the numerosity of the whole display, consistent

with their receiving inputs from many LIP neurons.

Thus, the Dehaene–Changeux model has plausibility, but considerable neurophysiological work will be needed to verify its key hypotheses about the role of LIP–VIP circuitry in invariant numerosity extraction. An important limit of the present data, which should be borne in mind, is that at present the two types of numerical codes (monotonic and tuned cells) have been found by different labs, in different areas, in different monkeys trained to perform different tasks. Thus, it is not known whether these two codes co-exist within the same animals.

It is interesting to note, however, that the LIP numerosity code uncovered in monkeys by Roitman et al. (2007) has all the properties needed to account for the recently discovered human numerosity adaptation effect discussed in the introduction (Burr & Ross 2008). Human numerosity adaptation is retinotopic, and it extends to across a large range of numbers: adaptation to 30 dots changes the perception of 400 dots, which would be impossible if number was encoded by cells tuned to these specific quantities, but makes sense if the adapted representation is a monotonic code. Thus, it is likely that humans also possess a monotonic numerosity code.

Roggeman et al. (2006) also presented priming evidence in support of the co-existence of two number codes in humans, compatible with the notion of monotonic versus tuned cells. They asked subjects to name, as quickly as possible, Arabic numerals or numerosities of sets of dots. In both cases, numbers ranged from 1 to 5, and each target was preceded by a brief but visible prime (83 ms), also from the same range, masked by a random-line pattern (49 ms). For Arabic numerals, priming depended symmetrically on the distance between the numbers, as previously observed with purely subliminal stimuli (Naccache & Dehaene 2001; Reynvoet, Brysbaert, & Fias 2002). For numerosities presented as sets of dots, however, priming showed an asymmetrical step function: nonsymbolic primes did not just facilitate the nearby num-

bers but in fact caused priming for all smaller numbers. This finding seems consistent with a monotonic code, with the additional specific property that increasing numbers of neurons are recruited as the number of items increases (Roggeman et al. 2006 term this a summation code). Very interestingly, these results suggest that the dominant code, which drives behavioral priming in humans, differs for symbolic versus nonsymbolic numbers: the tuned-cell code would be used for symbolic numerals, and some version of the monotonic cell code for numerosities presented as sets of objects. It remains to be seen, however, whether these priming results are not just due to counting processes deployed for small numbers, and how they can be reconciled with the fMRI evidence for tuned-cell priming with larger numerosities of sets of dots (Piazza et al. 2004).

Subitizing and Estimation

It is likely, indeed, that small numbers receive special treatment, implying that there must be yet other codes for number that underlie our strong arithmetic intuitions. For more than a century now, the small numbers 1, 2, and 3 have been thought to involve a partially distinct representational subsystem (Bourdon 1908; Feigenson et al. 2004; Jevons 1871). In human adults, the phenomenon of subitizing refers to the fact that these small numerosities 1, 2, and 3, when presented as sets of dots, can be very quickly and accurately identified and named, without the need for a deployment of serial attention in order to count (Piazza, Giacomini, Le Bihan, et al. 2003). Until recently, it was possible to maintain that this performance was perhaps due simply to the lower end of the estimation range—with small numbers, Weber’s law would ensure an excellent discrimination of 1 from 2 and 2 from 3, thus resulting in an apparent subitizing effect. This interpretation was strengthened by Nieder and Miller’s observation that, in the monkey IPS, all numerosities in the range 1–30 are seamlessly coded by cells with log-Gaussian tuning, and

that this coding scheme, which does not exhibit any discontinuity for small numbers, suffices to explain the monkey's behavior in numerical same–different tasks (Nieder & Miller 2003).

My laboratory, however, recently tested and rejected this interpretation of the human subitizing effect in a recent behavioral study (Revkin, Piazza, Izard, et al. 2008). We used a masked forced-choice paradigm in which participants named the numerosity of sets with either 1–8 or 10–80 items, matched for discrimination difficulty. The first case corresponds to the classical subitizing task. The second case is analogous in all respects, except that the numbers are all multiplied by 10. If Weber's law held, then participants should behave identically in the ranges 1–8 and 10–80, that is, they should have no difficulty in “subitizing” 10, 20, or 30 dots (once they know that only decade numbers are presented). The results, however, showed a clear violation of Weber's law, with a much higher precision over numerosities 1–4 in comparison to 10–40. These results argue against the single estimation system hypothesis and support the notion of a dedicated mechanism for apprehending small numerosities—a conclusion similar to that reached by developmental studies of infant numerical abilities (Feigenson et al. 2004). Although we currently have very little idea of how this system is organized at the neural level, it seems clear that a very quick and automatic grasp of the numerosities 1, 2, and 3 is part of the human intuition of numbers.

The Sense of Ordinality

A final aspect of number representation that seems to rely on a partially dissociable system is the sense of ordinality—the knowledge of which item in a fixed series comes first, second, third, and so on. Elegant experiments by Turconi and Seron have demonstrated that the ordinality and cardinality meanings of numbers, although often associated, are not synonymous to human subjects (Turconi, Campbell, & Seron 2006; Turconi, Jemel, Rossion, et al.

2004; Turconi & Seron 2002). Surprisingly, judging whether 2 is smaller than 5 is a different task than judging whether 2 comes before 5. The function that relates response times to numerical distance is distinct: it shows a classical distance for cardinality judgements (faster RTs with larger distances), but a partially reversed effect with ordinal judgements (fast RTs to consecutive pairs such as 4 and 5) (Turconi et al. 2006). Event-related potentials are also subtly different (Turconi et al. 2004), and knowledge of ordinality and cardinality, although often associated in brain-lesioned patients (Cipolotti et al. 1991), can be dissociated in Gerstmann's syndrome following a left parietal lesion (Turconi & Seron 2002).

Few studies to date have attempted to identify the cerebral bases of ordinal knowledge, but the available evidence suggests that ordinal and cardinal knowledge may involve partially different neural circuits within overlapping parietofrontal areas. Number comparison, which involves the cardinal meaning of numbers, and letter comparison, which involves ordinal knowledge, activate very similar parietofrontal networks in humans (Fias et al. 2007). Furthermore, during ordinal comparisons, the left intraparietal area shows a distance effect (smaller activation for more distant rank orders) which is very similar to that observed during number comparison (Marshuetz, Reuter-Lorenz, Smith, et al. 2006).

While the same overall regions are involved, recordings of single neurons in the IPS of macaque monkeys suggest that the fine-grained circuits are partially different (Nieder et al. 2006). When monkeys received either parallel or serial presentations of sets of dots, specific neurons tracked rank order during serial presentation, but very few of these neurons showed a joint sensitivity to the numerosity of simultaneously presented sets of dots. However, activation ultimately converged toward the same neural population for serial versus parallel presentations at the end of the sequence, when the final number was known and had to be held in working memory. Many other studies have

recorded from neurons sensitive to rank order in a variety of prefrontal, cingulate, frontal eye field, or caudate areas (for review, see Nieder 2005). For instance, Jean-Paul Joseph and his collaborators have repeatedly reported neurons that fire either to the first, the second, or the third action in a motor sequence, regardless of the particular action being performed (Procyk, Tanaka, & Joseph 2000). It remains unknown whether these same neurons would also be involved in cardinal number representation. All in all it seems that one must add ordinal representations to the list of number-relevant neural codes that are available to humans and other primates.

From Number Neurons to Arithmetic Intuitions

The Nieder–Miller studies suggest that cardinal number is encoded by a bank of neurons in area VIP, each tuned to a particular number. Furthermore, these studies are precise enough to quantitatively characterize, in a mathematical manner, the nature of the code. The firing rate of a numerosity-sensitive neuron that responds preferentially to numerosity p , in response to a range of stimulus numerosities n , traces a bell-shaped curve which is Gaussian on a log scale and has a maximal firing peak at the location p . All neurons seem to have a similar width of tuning (once plotted on a log scale)—there seems to be a single neural Weber fraction that defines the degree of coarseness with which neurons encode numerosity.

This code, which I term *log-Gaussian coding*, is remarkably similar to that postulated in the Dehaene and Changeux (1993) neural network model of numerosity processing: fMRI suggests that a very similar code is available in humans, in a plausibly homologous area (Piazza et al. 2004). I recently developed a detailed mathematical theory of how humans take decisions in number-related tasks, based on this underlying log-Gaussian code (Dehaene 2007). Assuming that this is the main neuronal code underlying

our sense of number, we can reconstruct, in a mathematical manner, most if not all of the properties of our intuitions of number during simple numerical cognition tasks.

Numerosity Discrimination and Comparison

The first and simplest set of tasks consists in deciding whether a certain number, presented as a set of dots, is equal to, larger than or smaller than a fixed numerical reference. The assumption that numerosity is represented by a random, Gaussian distribution of activation over an internal continuum (in this case the log of the input number) brings numerosity judgement within the realm of classical psychophysics and signal detection theory. It readily predicts that discrimination of two numerosities, as measured by d -prime, should improve linearly with distance on the logarithmic internal continuum (i.e., with the logarithm of the ratio of the two numbers), with the slope of that effect reflecting the Weber fraction (i.e., the degree of precision of the numerosity representation). Van Oeffelen and Vos (1982) tested this model against human numerosity discrimination data, and found it to be quite accurate. Manuela Piazza and I also verified this model in human adults during larger/smaller and same/different numerosity judgements (Piazza et al. 2004). Interestingly, the precision of discrimination varies during human development. Ratio-dependent performance has been observed during numerosity discrimination in human infants as early as 6 months of age (Lipton & Spelke 2003), but the Weber fraction appears to decrease with age: 6-month-old babies discriminate numerosities in a 2:1 ratio (Weber fraction of 1.0), but fail to discriminate numerosities in a 3:2 ratio (Weber fraction 0.5), while 9-month-old babies can (Lipton & Spelke 2003). Adults can discriminate numbers that are within 10%–15% of each other (Halberda & Feigenson 2008; Piazza et al. 2004; Pica et al. 2004). A recent study indicates that between 3 and 6 years of age, the Weber fraction decreases

smoothly with age, yet without achieving adult levels (Halberda & Feigenson 2008).

Recently, with Manuela Piazza and Marco Zorzi, we titrated the evolution of the Weber fraction using an identical numerosity comparison task in normally developing kindergartners, 10-year-olds, and young adults as well as dyscalculic children (Piazza et al., submitted). The log-Gaussian model provided an excellent fit to performance curves at all ages. Note that for kindergartners, the task was very difficult because the numbers to be compared were always within 25% of each other, and hence performance never exceeded 80% correct, even at the largest numerical distances. In this task, indeed, as in many psychophysical tasks, participants often have an impression of responding using only their “intuition,” but performance curves demonstrate that this intuition is not at all random and can be captured in great detail by our knowledge of numerosity coding in the parietal lobe. Furthermore, the Weber fraction decreased exponentially from about 0.40 at age 3 to 0.25 at age 10 and 0.15 in adults (results quantitatively similar to Halberda & Feigenson 2008). Most importantly, it was higher in dyscalculic children aged 8–12 years with severe deficits in arithmetic (mean Weber fraction = 0.34, comparable to kindergartners). Indeed, the Weber fraction predicted the severity of these children’s impairment in symbolic arithmetic tasks, but not in other domains such as word reading. Similar results by Halberda and Feigenson (2008) confirm that the psychophysics of numerosity discrimination can be a sensitive quantitative estimator of numerical understanding across development.

Response Times in Number Comparison

Signal detection theory is an idealized description and does not take into account the time taken to reach a decision. To simultaneously model decision times and error rates, more sophisticated models of accumulation of evidence have been proposed (for reviews, see Gold & Shadlen 2002; Link 1992; Smith

& Ratcliff 2004; Usher & McClelland 2001). These models assume that, in order to reach a decision, the brain needs to sequentially accumulate evidence toward each of the available response alternatives. Due to the inescapable presence of sources of noise in the nervous system (either in the input, in its internal representation by noisy neurons, or in the decision mechanism itself), the accumulated evidence will vary in time as well as from trial to trial, forming a “random walk.” Most current models assume that a firm decision is reached, and the motor response is launched, only once the accumulated evidence in favor of one of the alternatives has reached a critical threshold.

Assuming a log-Gaussian internal coding of number, it is possible to derive mathematical equations relating response time, error rate, and numerical distance in simple numerical tasks of larger/smaller comparison and same/different judgements (for details and equations, see Dehaene 2007). As already noted by Link (1975, 1990, 1992), the accumulation of evidence or diffusion-to-bound model provides a compact account of many aspects of the number comparison data. For error rates, the model predicts a logistic function of distance on the internal continuum, which is virtually indistinguishable from the error function (integral of a Gaussian) predicted by signal detection theory. For response times, however, the model correctly predicts a dependency on numerical distance that is less peaked than the error curve and is well approximated by an inverse function. The model also predicts a specific linear relation between response times and a transformed function of error rates.

For the sake of illustration, Figure 4 plots data from an experiment by Cantlon and Brannon (2006), in which the very same behavioral task of numerosity comparison was applied to macaque monkeys and adult humans. Two monkeys and 11 human subjects were presented with arrays of dots ranging from 2 to 30 dots, and had to select the smaller array or, in other blocks, the larger array. Figure 4 shows the averaged data and fits of the accumulation

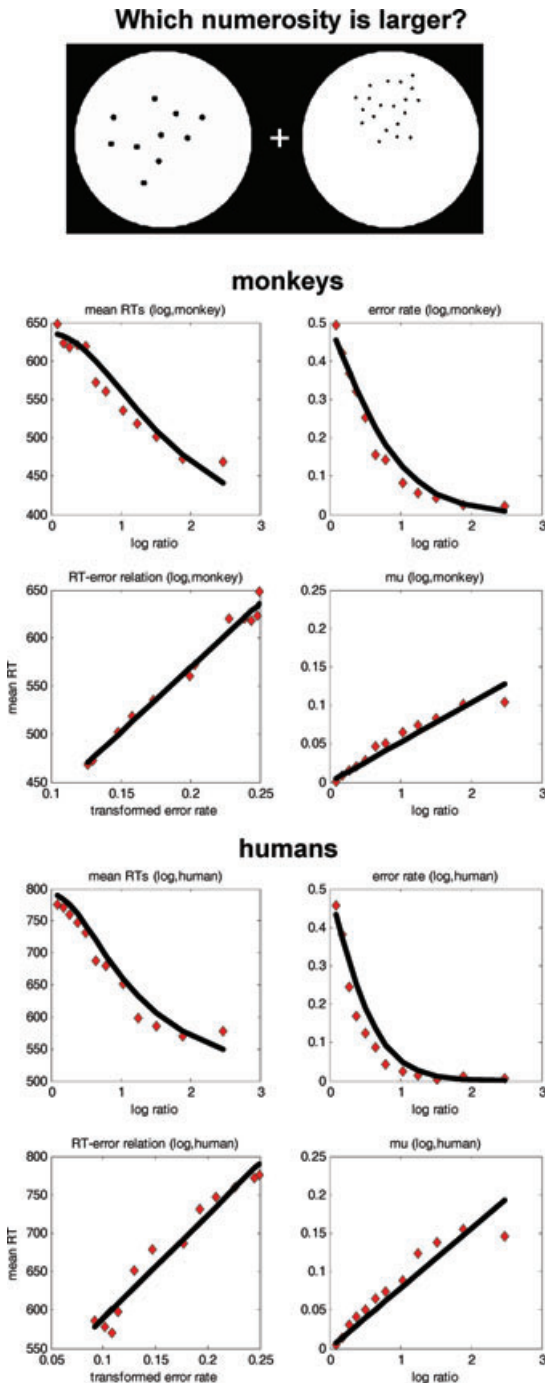


Figure 4. Mathematical modeling of response times and error rates during a numerosity comparison task (data from Cantlon & Brannon 2006). For both monkeys and humans, panels illustrate the dependency of RTs (*top left*) and errors (*top right*) on distance between the numbers, measured by the log of their ratio (i.e., the distance between their logarithmic internal representations). The *bottom*

of evidence model. The accumulation of evidence model has only three free parameters (nondecision time, slope of accumulation as a function of the difference in logs of the two numbers, and decision boundary). Although the quantitative fit is not perfect, this model clearly suffices to capture many qualitative features of performance, including the shape of RTs, error rates, and their interrelations.

It should also be noted that, with only one additional hypothesis, the accumulation of evidence model can also account for how performance changes when the number-comparison task is performed concurrently with another task in a dual-task or “psychological refractory period” setting. The only new hypothesis is that the decision stage creates a serial bottleneck in processing, while predecision (sensory) and postdecision (motor) stages can operate in parallel for the two tasks (for details, see Sigman & Dehaene 2005, 2006).

Numerosity Labeling and Naming

A more complex task consists in asking subjects to label numerosities using a set of symbols, either Arabic numerals or number words. For instance, one may ask human subjects to name sets of dots ranging from 10 to 100 with round numbers such as the decade names “ten” to “ninety” (Izard 2005). As exemplified in Figures 1 and 2, this is not necessarily an easy task, but once again, subjects are ready to venture an “intuitive” response, which turns out to be tightly correlated with the actual numerosity. Even chimpanzees can be trained to label numerosities using the Arabic digits 1 through

left panel shows the relation between mean RT and transformed error rates predicted by the accumulation of evidence model (for details, see Dehaene 2007; Link 1992). The *bottom right* panel shows how the amount of evidence accumulated at each time step, inferred from a fit of the accumulation of evidence model, varies linearly with log ratio, as was expected according the log-Gaussian coding scheme.

9 (Matsuzawa 1985; Tomonaga & Matsuzawa 2002).

The theory for such numerosity labeling tasks, developed by Véronique Izard (2005; Izard & Dehaene 2008), assumes that subjects simply map segments of their internal log-Gaussian continuum onto the requested response labels. Humans, of course, can deploy more complex counting strategies, but these can be discouraged by fast stimulus presentation times and avoidance of very small numbers. In animals, and perhaps also in human cultures with few number words and no overt counting system, the assumption that subjects do not count serially, but merely apply symbolic labels to their mental representations of approximate numerosity, seems realistic (Dehaene & Mehler 1992; Gordon 2004; Pica et al. 2004; Tomonaga & Matsuzawa 2002). The theory therefore assumes that, for each target numerosity n , subjects generate an internal distribution of activation on the log-Gaussian internal continuum and respond with the verbal label r whose position on the number line $\text{Log}(r)$ falls closest to $\text{Log}(n)$. This strategy implies that the number line continuum is divided into distinct response domains according to a set of response criteria forming a response grid.

One difficulty is that subjects' responses are often poorly calibrated and underestimate the true numerosity. For instance, as you may judge for yourself in Figure 1, it is quite common to respond "fifty" to a set of 100 or 200 dots (Krueger 1982; Minturn & Reese 1951). While the origins of this illusion remain unknown, Véronique Izard showed that it could be captured by a simple assumption: subjects use an affine rescaling of their response grid, referring to location $a \text{Log}(r) + b$ instead of $\text{Log}(r)$ for response r . The above model provided a remarkably good fit to human subjects' numerosity naming data in the range 10–100 (Izard & Dehaene 2008). All subjects were initially miscalibrated and severely underestimated numerosity. In those cases, the model predicts a power law relation between the presented numerosity and the subject's mean response, which is ex-

actly what was observed. A single example of a numerosity–name pairing was sufficient to recalibrate the responses to a quasilinear relation, a process that was well captured by a change in the parameters a and b .

The numerosity labeling model supposes the existence of a rapid association process that can quickly convert a quantity to the corresponding verbal or Arabic symbol, or vice versa. Indeed, there is now considerable evidence that such a conversion process exists and can be extremely rapid and automatic (Piazza et al. 2007). Perhaps most relevant to the concept of arithmetical intuition, there is evidence that access to the quantity representation from number symbols is sufficiently efficient to occur without consciousness. A flashed digit or number word, masked by letter or symbol strings that make it subjectively invisible, can nevertheless prime a subsequent visible digit during a number comparison task (Dehaene et al. 1998). In this paradigm, the bilateral IPS shows fMRI repetition suppression when the same number is presented twice, even when the input notation differs (e.g., "ONE" followed by 1) (Naccache & Dehaene 2001). Behavioral studies show that priming depends monotonically on the numerical distance between the prime and the target, being larger for the pair ONE \rightarrow 1 than for TWO \rightarrow 1, THREE \rightarrow 1, or FOUR \rightarrow 1 (Reynvoet et al. 2002). Altogether, these findings suggest that the parietal quantity representation can be contacted nonconsciously by the mere sight of a digit or number word—there is, thus, a form of "second-order" intuition for number symbols, which is created by associating these arbitrary labels to meaningful quantities.

Changes in Arithmetic Intuitions Induced by the Acquisition of Number Symbols

Does the acquisition of expertise with number symbols solely consist in the laying down of a mapping with preexisting representations of quantity? A recent neural network of the

numerosity labeling process suggests otherwise and implies that symbol acquisition may lead to deeper changes in the quantity system (Verguts & Fias 2004). Verguts and Fias used nonsupervised learning in a network exposed either to numerosity information alone or to numerosity paired with an approximate symbol. When nonsymbolic information alone was presented, the network developed numerosity detectors similar to Nieder and Miller's neurons: they exhibited tuning curves that had a Gaussian shape with fixed width when plotted on a logarithmic numerosity axis. After pairing of the nonsymbolic numerosity inputs with symbolic information, the numerosity detector units became tuned to symbols as well, but with two key differences. First, the tuning curves were much sharper when symbolic inputs were provided: the simulated neurons essentially had a discrete peak of firing at their preferred value, with only a small distance effect for other numbers. Second, the tuning curves now exhibited a fixed width for all the numbers tested (1 through 5). Thus, the network developed a new type of representation, *linear with fixed variability*.

Verguts and Fias's proposal has the potential to explain several aspects of human intuition for number symbols. Once the mapping is learned, there would be instantaneous transfer across nonsymbolic and symbolic formats of inputs—explaining for instance that preschoolers perform better than chance with additions and subtractions of large numbers presented in symbolic form (Gilmore et al. 2007). Because the neurons' tuning curve is narrower for symbolic than for nonsymbolic inputs, calculation would be much more precise with the former than with the latter. For instance, errors in number comparison would be much more frequent with nonsymbolic than with symbolic stimuli, and performance should depend on the ratio of the numbers in the former case and on the linear distance in the latter—two predictions that are upheld in actual data (for details, see Dehaene 2007).

Manuela Piazza, Philippe Pinel, and I recently used fMRI adaptation to test directly

the hypothesis of a common parietal code for symbolic numerals and nonsymbolic numerosities (Piazza et al. 2007). For a whole fMRI run, subjects attended to the repeated presentation of an approximate quantity presented either as a set of dots (e.g., 17, 18, or 19 dots) or as an Arabic numeral (the numerals 17, 18, or 19). As expected, within intraparietal regions isolated using an independent subtraction task, the fMRI signal adapted over the course of about 40 sec. We then introduced sparse deviants that could be close or far from the adaptation value (e.g., 20 or 50) and that appeared either in the same or in a different notation. The intraparietal cortex signal showed a distance-dependent recovery from adaptation which, crucially, was observed even when the numerical notation changed from dots to Arabic and vice versa, indicating that there must be populations of numerosity detector neurons coding for numerical quantity independently of the symbolic or nonsymbolic format of input.

Interestingly however, in left parietal cortex, the effect was asymmetrical. When adaptation was to dots and the deviants were Arabic numerals, there was recovery of adaptation to far but not to close quantities. However, when adaptation was to Arabic numerals and the deviants were dots, there was recovery of adaptation to both close and far quantities (e.g., adaptation to 17, 18, 19, recovery to both 20 and 50). This finding suggests that the quantities evoked by Arabic numerals may be more precise than those evoked by nonsymbolic sets of dots. Hence, in the left hemisphere at least, the neuronal populations adapted by Arabic stimuli may be narrower than those evoked by dots presentations, as proposed in Verguts and Fias's (2004) model. The right-hemispheric intraparietal region, perhaps because it is not in direct interconnection with left-hemispheric language areas, seems to exhibit a much lesser influence of exposition to number symbols, if any.

The idea that acquisition of number symbols improves the representation of numbers in the left parietal lobe receives support from several sources. First, developmental fMRI studies

point to left parietal cortex as a crucial site whose activity changes during arithmetic development, compatible with the hypothesis that this region serves as a hub where abstract quantity information meets with left-hemispheric codes for Arabic and verbal number symbols (Dehaene & Cohen 1995). Ansari and Dhital (2006) observed a greater effect of the distance between numbers during a comparison task in this region in adults compared to 10-year-olds, suggesting an increasing involvement of this region with increasing age. By imaging children of different ages during an identical arithmetic task, Rivera et al. (2005) observed increasing activation with age in the left parietal and left lateral occipitotemporal cortex, compatible with the hypothesis that these areas respectively come to encode numerical quantities and number symbols with increasingly refined precision.

Language and arithmetic are jointly lateralized to the left hemisphere in the majority of right-handed adults. The above developmental model suggests that this “colateralization” reflects a causal interaction during developmental, with language lateralization preceding and causing a progressively increasing lateralization of numerical representations in the parietal lobe. Recently, Philippe Pinel and I put this theory to a test using a large database of fMRI data during spoken language processing and calculation (Pinel et al. 2009). We designed a “colateralization analysis” over 209 healthy subjects, investigating whether variations in the degree of left-hemispheric asymmetry that characterize the brain organization for language are mirrored in the asymmetry of areas involved in number processing. As predicted, we observed that the degree of asymmetry in the activation of the posterior superior temporal sulcus during a sentence-reading task correlates strongly and selectively with the degree of asymmetry of calculation-induced activation in the intraparietal sulcus. This finding is compatible with the hypothesis that during childhood education, hemispheric asymmetries for language partially alter the organization of the brain networks for arithmetic.

Very recently, the issue of how cultural symbols modify the organization of the neural networks for number has become addressable in the monkey. Diester and Nieder (2007) presented the first study of the cerebral mechanisms of number symbol acquisition in non-human primates. They trained two monkeys on a symbolic match-to-sample task that required matching the shape of an Arabic numeral, ranging from 1 to 4, to the corresponding numerosity of a set of dots. In dorsolateral prefrontal cortex, Diester and Nieder found many neurons that coded for number independently of the symbolic or nonsymbolic notation used to convey it. Each neuron had a similar tuning curve for number, regardless of the format of presentation. Surprisingly however, in intraparietal cortex the vast majority of neurons were specialized either for Arabic numerals or for numerosities, but not both. Thus, only dorsolateral prefrontal cortex seemed capable of encoding the arbitrary relation between symbols and their numerical meaning. In humans, considerable training may ultimately lead to a transfer to specialized posterior brain systems. In the Rivera et al. (2005) fMRI study of arithmetic development, indeed, a massive decrease was observed in prefrontal activity as a function of age, suggesting that the automatization of mental arithmetic is accompanied by a progressive transfer from anterior generic to posterior specialized circuits.

Linking Numbers to Space

A final aspect of human numerical intuition that seems to be heavily influenced by education and cultural background is the linking of numbers with space. This mapping plays an essential role in mathematics, from measurement and geometry to the study of irrational numbers, Cartesian coordinates, the real number line, and the complex plane. In most human adults, the mere presentation of an Arabic numeral automatically elicits a spatial bias in both motor responding and attention orienting

(Dehaene, Bossini, & Giraux 1993; Fischer, Castel, Dodd, et al. 2003; Hubbard et al. 2005; Zorzi, Priftis, & Umiltà 2002): even when performing a task as simple as deciding whether a digit is odd or even, or whether it is larger or smaller than 5, small numbers are automatically mapped to the left side of space, and large numbers to the right side Spatial-Numerical Association of Response Codes, or (SNARC effect).

We recently reported a similar systematic interference pattern during mental arithmetic, which we termed “operational momentum,” and which suggests that a spatial code and a sense of motion are automatically activated during mental arithmetic (Knops, Viarouge, & Dehaene 2009; McCrink, Dehaene, & Dehaene-Lambertz 2007). When subjects were shown two successive sets of dots and asked to approximate their sum or their difference, their estimates always overshot the correct outcomes, as if they moved “too far” toward large numbers during addition, and too far toward small numbers during subtraction. A small but similar effect was found with symbolic additions and subtractions of two-digit Arabic numerals. Furthermore, when picking one out of several plausible results displayed on a computer screen, participants were spatially biased toward selecting choices that appeared on the top right side of screen during addition, and on the top left during subtraction.

These momentum and numerical–spatial interference effects may originate from the fact that the intraparietal region, which is active during number processing and calculation, is remarkably close and often overlapping with areas engaged in the coding of spatial dimensions such as size, location, and gaze direction (Hubbard et al. 2005; Pinel et al. 2004; Simon et al. 2002). In particular, the putative human homolog of area LIP is also active during some number processing tasks (Dehaene, Piazza, Pinel, et al. 2003), fueling the speculation that the VIP–LIP circuitry is partially recycled for mental arithmetic in humans (Hubbard et al. 2005). We recently used fMRI to demon-

strate a numerical interference effect in the putative human homolog of area LIP (Hubbard, Pinel, Jobert, et al. 2008): during the classical SNARC task (parity judgment), large numbers evoked slightly more activation in left LIP, consistent with a rightward shift of attention in space, while small numbers evoked slightly more activation in right LIP.

Although there is considerable evidence that number–space mappings are an integral part of numerical intuition, the exact shape of this mapping seems to be heavily influenced by culture and education. First, the direction of the number–space association—small numbers to the left, large numbers to the right—varies with the cultural environment, particularly the direction of reading, as it tends to be reduced, canceled, or even reversed in right-to-left readers (Dehaene et al. 1993; Shaki & Fischer 2008; Zebian 2005). Indeed, multiple mappings may co-exist in the same individual: Chinese readers preferentially associate Arabic numerals with the horizontal axis, and Chinese number words with the vertical axis (Hung, Hung, Tzeng, et al. 2008). Second, recent experiments have documented a remarkable developmental shift in children’s conception of how numbers map onto space (Booth & Siegler 2006; Siegler & Booth 2004; Siegler & Opfer 2003). When asked to point toward the correct location for a spoken number word on a line segment labeled with 1 at left and 100 at right, even kindergarteners understand the task and behave nonrandomly, systematically placing smaller numbers at left and larger numbers at right. However, they do not distribute the numbers evenly in a linear manner. Rather, they devote more space to small numbers, thus imposing a compressed and seemingly logarithmic mapping. For instance they will place number 10 near the middle of the interval 1 through 100. Beran et al. (2008) recently reported similar logarithmic responding with a bisection task in monkeys and 4- to 5-year-old children. A shift from logarithmic to linear mapping occurs later in development, between first and fourth grade, depending on experience and the

range of numbers tested (Booth & Siegler 2006; Siegler & Booth 2004; Siegler & Opfer 2003). My colleagues and I recently showed that this shift depends on culture and education: it does not occur spontaneously in the Mundurucu, even in adult subjects and even in the range of numbers 1 to 10 (Dehaene, Izard, Spelke, et al. 2008). The Mundurucu do have strong intuitions of number–space mappings, since they can systematically map numbers to a segment bearing the numerosities 1 and 10 in a monotonic manner. However, their responses are logarithmically spaced. Even bilingual adults who could count in Portuguese, although they mapped Portuguese words onto the line segment in a linear manner, still mapped sets of dots and Mundurucu number words using a logarithmic scale.

This compressive, logarithmic response can be easily explained by the log-Gaussian model. One must merely assume that subjects report a rating of the psychological distance of each number to the endpoints of the segment. On the log scale, distance covaries with numerical ratio. For instance, 3 is equally distant from 1 and from 9 because these numbers are all in a 3:1 ratio. Thus, it is natural or “intuitive” for the Mundurucu and for young children to place 3 in the middle of 1 and 9. The progressive replacement of this intuitive similarity scale by a linear scale is compatible with Verguts and Fias’s (2004) model, in which exposure to number symbols sharpens neural tuning until all neurons have a fixed width irrespective of the size of the numbers involved, so that Weber’s law no longer applies to symbolic numerals when they are represented at this conceptual level. As discussed above, it is tempting to speculate that this sharpening and linearization effect only occurs in the left but not in the right parietal cortex. Such a co-existence of logarithmic and linear representations of numbers, even within the brains of educated adults, would explain why even American adults continue to judge that 5 is more similar to 9 than to 1, with a similarity metric that is captured by a logarithmic scale

(Shepard, Kilpatrick, & Cunningham 1975). It would also account for why adults are unable to rate whether a sequence of random numbers is spread equally across the number continuum—they always rate as “most random” a sequence that oversamples small numbers, as if they were sampling from a compressive internal continuum (Banks & Coleman 1981; Viarouge, Hubbard, Dehaene, et al. 2008).

The present emphasis on number–space interactions should not be taken to deny that other types of automatic associations also contribute to our arithmetic intuition. Considerable behavioral evidence indicates a tight and automatic link between number and the location and size of hand movements (Andres, Davare, Pesenti, Olivier, et al. 2004; Andres, Ostry, Nicol, et al. 2008; Lindemann, Abolafia, Girardi, et al. 2007; Moretto & di Pellegrino 2008; Song & Nakayama 2008). Fingers and numbers are of course highly associated by counting practices in the course of arithmetic development, and this is reflected in automatic number–finger associations in human adults (Andres, Seron, & Olivier 2007; Di Luca, Grana, Semenza, et al. 2006; Sato, Cattaneo, Rizzolatti, et al. 2007), although number–space interactions appear to dominate over number–finger associations when the two are in conflict (Brozzoli et al. 2008). Although the neurophysiological basis of number–hand interactions is currently unknown, it is tempting to speculate that it arises from interactions between numerical representations in the hIPS and representations of hand shape during grasping in the nearby area AIP (see Fig. 3). Indeed, activation is occasionally reported at the location of the putative human homolog of area AIP during number processing (e.g., Fias et al. 2007; Hubbard et al. 2005). Through its central location in the parietal lobe and its high interconnectivity with the surrounding regions, the hIPS certainly has many opportunities for learning associations of number with other spatial and movement-related domains in the course of arithmetic development.

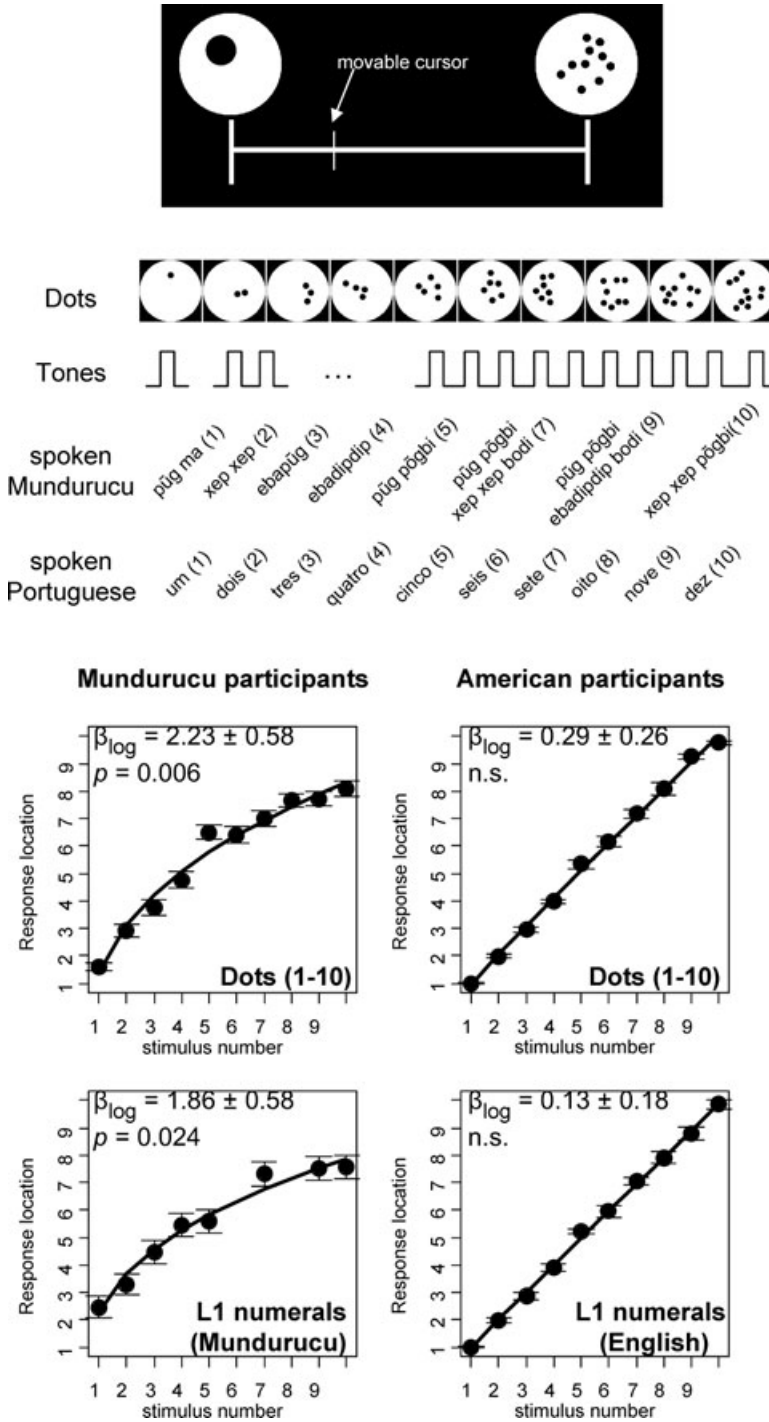


Figure 5. Number-space mapping task used in the Mundurucu (after Dehaene et al. 2008). Each target number was presented as a set of dots, a stream of tones, or a Mundurucu or Portuguese number word (note that we used very rarely uttered Mundurucu expressions for 7 and 9). Participants were asked to point to the corresponding location on the number line. The sample data shown at bottom illustrate that the Mundurucu participants understood the task and mapped numbers systematically, yet with a logarithmic scale, which was not seen in control American participants.

Conclusion

Our arithmetic intuition consists of a complex web of knowledge, ranging from the quick assessment of the approximate numerosity of 30 dots to the realization that numerosity must change when elements are added to a set, or to the immediate realization that 8 is larger than 3 and that $13 + 34 = 97$ is false. Our intuition is not even necessarily consistent, as when we judge that 5 is more similar to 9 than to 1, yet falls in the middle of the 1–9 interval. In the past 20 years, research has consistently demonstrated that the core of our intuition—a logarithmic sense of approximate numerosity—finds its origin in an internal representation of numbers that dates back to our infancy, that we share with other animal species, and that relates to a bilateral parietal circuitry. Much less clear is how this intuition gets transformed and refined in the course of education. Experience with number symbols, counting, and measurement probably all contribute to the “linearization” of our numerical intuition—the shift from an informal logarithmic representation of approximate numerosity to a formal, symbolic, linear representation of number and arithmetic. In this chapter, I speculated that this transformation relates to the progressive transformation of number codes, particularly in the left parietal lobe, “recycling” this region until it can be accessed automatically through the arbitrary cultural symbols of Arabic numerals (Dehaene & Cohen 2007). I also proposed that a dormant logarithmic code may remain present in right intraparietal cortex. Future research should concentrate on the empirical testing of these two hypotheses, but also on the important issue of how arithmetic intuition can be fostered by classroom practice in normal as well as dyscalculic children.

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Conflicts of Interest

The author declares no conflicts of interest.

References

- Andres, M., Davare, M., Pesenti, M., et al. (2004). Number magnitude and grip aperture interaction. *Neuroreport*, *15*(18), 2773–2777.
- Andres, M., Ostry, D. J., Nicol, F., et al. (2008). Time course of number magnitude interference during grasping. *Cortex*, *44*(4), 414–419.
- Andres, M., Seron, X., & Olivier, E. (2007). Contribution of hand motor circuits to counting. *J. Cogn. Neurosci.*, *19*(4), 563–576.
- Ansari, D., & Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: an event-related functional magnetic resonance imaging study. *J. Cogn. Neurosci.*, *18*(11), 1820–1828.
- Antell, S.E., & Keating, D. P. (1983). Perception of numerical invariance in neonates. *Child Dev.*, *54*, 695–701.
- Appolonio, I., Rueckert, L., Partiot, A., et al. (1994). Functional magnetic resonance imaging (fMRI) of calculation ability in normal volunteers. *Neurol.*, *44*, 262.
- Banks, W. P., & Coleman, M. J. (1981). Two subjective scales of number. *Percept. Psychophysics*, *29*, 95–105.
- Barth, H., La Mont, K., Lipton, J., et al. (2006). Nonsymbolic arithmetic in adults and young children. *Cognition*, *98*(3), 199–222.
- Beran, M. J., Johnson-Pynn, J. S., & Ready, C. (2008). Quantity representation in children and rhesus monkeys: linear versus logarithmic scales. *J. Exp. Child Psychol.*, *100*(3), 225–233.
- Berger, A., Tzur, G., & Posner, M. I. (2006). Infant brains detect arithmetic errors. *Proc. Natl. Acad. Sci. USA*, *103*(33), 12649–12653.
- Bijeljac-Babic, R., Bertoncini, J., & Mehler, J. (1991). How do four-day-old infants categorize multisyllabic utterances. *Dev. Psychol.*, *29*, 711–721.
- Booth, J. L., & Siegler, R. S. (2006). Developmental and individual differences in pure numerical estimation. *Dev. Psychol.*, *42*(1), 189–201.

- Bourdon, B. (1908). Sur le temps nécessaire pour nommer les nombres. *Revue philosophique de la France et de l'étranger*, 65, 426–431.
- Bremmer, F., Schlack, A., Shah, N. J., et al. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29(1), 287–296.
- Brozzoli, C., Ishihara, M., Gobel, S. M., et al. (2008). Touch perception reveals the dominance of spatial over digital representation of numbers. *Proc. Natl. Acad. Sci. USA*, 105(14), 5644–5648.
- Burr, D., & Ross, J. (2008). A visual sense of number. *Curr. Biol.*, 18(6), 425–428.
- Butterworth, B., Reeve, R., Reynolds, F., et al. (2008). Numerical thought with and without words: Evidence from indigenous Australian children. *Proc. Natl. Acad. Sci. USA*, 105(35), 13179–13184.
- Cantlon, J. F., & Brannon, E. M. (2006). Shared system for ordering small and large numbers in monkeys and humans. *Psychol. Sci.*, 17(5), 401–406.
- Cantlon, J. F., Brannon, E. M., Carter, E. J., et al. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biol.*, 4(5), e125.
- Castelli, F., Glaser, D. E., & Butterworth, B. (2006). Discrete and analogue quantity processing in the parietal lobe: a functional MRI study. *Proc. Natl. Acad. Sci. USA*, 103(12), 4693–4698.
- Chochon, F., Cohen, L., van de Moortele, P. F., et al. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. *J. Cog. Neurosci.*, 11, 617–630.
- Cipolotti, L., Butterworth, B., & Denes, G. (1991). A specific deficit for numbers in a case of dense acalculia. *Brain*, 114, 2619–2637.
- Cohen Kadosh, R., & Henik, A. (2006). A common representation for semantic and physical properties: a cognitive-anatomical approach. *Exp. Psychol.*, 53(2), 87–94.
- Cohen Kadosh, R., Henik, A., Rubinsten, O., et al. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, 43(9), 1238–1248.
- Condry, K. F., & Spelke, E. S. (2008). The development of language and abstract concepts: the case of natural number. *J. Exp. Psychol. Gen.*, 137(1), 22–38.
- Cordes, S., & Brannon, E. M. (2008). The difficulties of representing continuous extent in infancy: using number is just easier. *Child Dev.*, 79(2), 476–489.
- Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? *Neuropsychologia*, 44(13), 2668–2684.
- Davis, P. J., Hersh, R., & Marchisotto, E. A. (1995). *The Mathematical Experience*. Boston: Birkhauser.
- Dehaene, S. (1997). *The Number Sense*. New York: Oxford University Press.
- Dehaene, S. (2007). Symbols and quantities in parietal cortex: Elements of a mathematical theory of number representation and manipulation. In P. Haggard & Y. Rossetti (Eds.), *Attention & Performance XXII. Sensori-Motor Foundations of Higher Cognition* (pp. 527–574). Cambridge, MA: Harvard University Press.
- Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and numerical magnitude. *J. Exp. Psychol. Gen.*, 122, 371–396.
- Dehaene, S., & Changeux, J. P. (1993). Development of elementary numerical abilities: A neuronal model. *J. Cog. Neurosci.*, 5, 390–407.
- Dehaene, S., & Cohen, L. (1995). Towards an anatomical and functional model of number processing. *Math Cog*, 1, 83–120.
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, 56(2), 384–398.
- Dehaene, S., Izard, V., Spelke, E., et al. (2008). Log or linear? Distinct intuitions of the number scale in Western and Amazonian indigene cultures. *Science*, 320(5880), 1217–1220.
- Dehaene, S., & Mehler, J. (1992). Cross-linguistic regularities in the frequency of number words. *Cognition*, 43, 1–29.
- Dehaene, S., Naccache, L., Le Clec'H, G., et al. (1998). Imaging unconscious semantic priming. *Nature*, 395, 597–600.
- Dehaene, S., Piazza, M., Pinel, P., et al. (2003). Three parietal circuits for number processing. *Cog. Neuropsychol.*, 20, 487–506.
- Dehaene, S., Spelke, E., Pinel, P., et al. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science*, 284(5416), 970–974.
- Dehaene, S., Tzourio, N., Frak, V., et al. (1996). Cerebral activations during number multiplication and comparison: a PET study. *Neuropsychologia*, 34, 1097–1106.
- Delazer, M., Domahs, F., Bartha, L., et al. (2003). Learning complex arithmetic—an fMRI study. *Brain Res. Cogn. Brain Res.*, 18(1), 76–88.
- Di Luca, S., Grana, A., Semenza, C., et al. (2006). Fingert-digit compatibility in Arabic numeral processing. *Quart. J. Exp. Psychol. (Colchester)*, 59(9), 1648–1663.
- Diestler, I., & Nieder, A. (2007). Semantic associations between signs and numerical categories in the prefrontal cortex. *PLoS Biol.*, in press.
- Eger, E., Sterzer, P., Russ, M. O., et al. (2003). A supramodal number representation in human intraparietal cortex. *Neuron*, 37(4), 719–725.
- Feigenson, L. (2005). A double-dissociation in infants' representations of object arrays. *Cognition*, 95(3), B37–B48.

- Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends Cogn. Sci.*, 8(7), 307–314.
- Fias, W., Lammertyn, J., Caessens, B., et al. (2007). Processing of abstract ordinal knowledge in the horizontal segment of the intraparietal sulcus. *J. Neurosci.*, 27(33), 8952–8956.
- Fias, W., Lammertyn, J., Reynvoet, B., et al. (2003). Parietal representation of symbolic and nonsymbolic magnitude. *J. Cogn. Neurosci.*, 15(1), 47–56.
- Fischer, M. H., Castel, A. D., Dodd, M. D., et al. (2003). Perceiving numbers causes spatial shifts of attention. *Nat. Neurosci.*, 6(6), 555–556.
- Gelman, R., & Butterworth, B. (2005). Number and language: how are they related? *Trends Cogn. Sci.*, 9(1), 6–10.
- Gelman, R., & Gallistel, C. R. (1978). *The Child's Understanding of Number*. Cambridge, MA: Harvard University Press.
- Gilmore, C. K., McCarthy, S. E., & Spelke, E. S. (2007). Symbolic arithmetic knowledge without instruction. *Nature*, 447(7144), 589–591.
- Gold, J. I., & Shadlen, M. N. (2002). Banburismus and the brain: decoding the relationship between sensory stimuli, decisions, and reward. *Neuron*, 36(2), 299–308.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends Neurosci.*, 15, 20–25.
- Gordon, P. (2004). Numerical cognition without words: Evidence from Amazonia. *Science*, 306, 496–499.
- Hadamard, J. (1945). *An Essay on the Psychology of Invention in the Mathematical Field*. Princeton, NJ: Princeton University Press.
- Halberda, J., & Feigenson, L. (2008). Developmental change in the acuity of the “number sense”: The approximate number system in 3-, 4-, 5-, and 6-year-olds and adults. *Dev. Psychol.*, 44(5), 1457–1465.
- Halberda, J., Mazocco, M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, 455(7213), 665–668.
- Holloway, I. D., & Ansari, D. (2008). Mapping numerical magnitudes onto symbols: The numerical distance effect and individual differences in children's mathematics achievement. *J. Exp. Child Psychol.*, in press.
- Hubbard, E., Pinel, P., Jobert, A., et al. (2008). The place for the SNARC: Interactions between numerical and spatial representations in parietal cortex. submitted.
- Hubbard, E., Pinel, P., Jobert, A., et al. (2008). Topographical and functional relations between calculation, multisensory processing and eye-movements in the human brain. submitted.
- Hubbard, E. M., Piazza, M., Pinel, P., et al. (2005). Interactions between number and space in parietal cortex. *Nat. Rev. Neurosci.*, 6(6), 435–448.
- Hung, Y. H., Hung, D. L., Tzeng, O. J., et al. (2008). Flexible spatial mapping of different notations of numbers in Chinese readers. *Cognition*, 106(3), 1441–1450.
- Ischebeck, A., Zamarian, L., Siedentopf, C., et al. (2006). How specifically do we learn? Imaging the learning of multiplication and subtraction. *NeuroImage*, 30(4), 1365–1375.
- Izard, V. (2005). *Interactions between verbal and non-verbal numerical representations: theoretical and empirical approaches*. Unpublished PhD thesis, University of Paris VI, Paris.
- Izard, V., Dehaene-Lambertz, G., & Dehaene, S. (2008). Distinct cerebral pathways for object identity and number in human infants. *PLoS Biol.*, 6, e11.
- Izard, V., & Dehaene, S. (2008). Calibrating the mental number line. *Cognition*, 106(3), 1221–1247.
- Jevons, W. S. (1871). The power of numerical discrimination. *Nature*, 3, 281–282.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.*, 17, 4302–4311.
- Kaufmann, L., Koppelstaetter, F., Delazer, M., et al. (2005). Neural correlates of distance and congruity effects in a numerical Stroop task: an event-related fMRI study. *NeuroImage*, 25(3), 888–898.
- Knops, A., Viarouge, A., & Dehaene, S. (2009). Dynamic representations underlying symbolic and non-symbolic calculation: Evidence from the operational momentum effect. *Percept. & Psychophysics*, in press.
- Krueger, L. E. (1982). Single judgments of numerosity. *Percept. Psychophysics*, 31, 175–182.
- Le Corre, M., & Carey, S. (2007). One, two, three, four, nothing more: an investigation of the conceptual sources of the verbal counting principles. *Cognition*, 105(2), 395–438.
- Lee, K. M. (2000). Cortical areas differentially involved in multiplication and subtraction: A functional magnetic resonance imaging study and correlation with a case of selective acalculia. *Ann. Neurol.*, 48, 657–661.
- Lemer, C., Dehaene, S., Spelke, E., et al. (2003). Approximate quantities and exact number words: Dissociable systems. *Neuropsychologia*, 41, 1942–1958.
- Lindemann, O., Abolafia, J. M., Girardi, G., et al. (2007). Getting a grip on numbers: numerical magnitude priming in object grasping. *J. Exp. Psychol. Hum. Percept. Perform.*, 33(6), 1400–1409.
- Link, S. W. (1975). The relative judgment theory of two choice response time. *J. Math Psychol.*, 12, 114–135.
- Link, S. W. (1990). Modelling imageless thought: The relative judgment theory of numerical comparisons. *J. Math Psychol.*, 34, 2–41.
- Link, S. W. (1992). *The Wave Theory of Difference and Similarity*. Hillsdale, NJ: Erlbaum.

- Lipton, J., & Spelke, E. (2003). Origins of number sense: Large number discrimination in human infants. *Psycho. Sci.*, *14*, 396–401.
- Lipton, J. S., & Spelke, E. S. (2006). Preschool children master the logic of number word meanings. *Cognition*, *98*(3), B57–B66.
- Marshuetz, C., Reuter-Lorenz, P. A., Smith, E. E., et al. (2006). Working memory for order and the parietal cortex: an event-related functional magnetic resonance imaging study. *Neurosci.*, *139*(1), 311–316.
- Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature*, *315*(6014), 57–59.
- McCrink, K., Dehaene, S., & Dehaene-Lambertz, G. (2007). Moving along the number line: Operational momentum in non-symbolic arithmetic. *Percept. Psychophys.*, *69*(8), 1324–1333.
- McCrink, K., & Wynn, K. (2004). Large-number addition and subtraction by 9-month-old infants. *Psychol. Sci.*, *15*(11), 776–781.
- Minturn, A. L., & Reese, T. W. (1951). The effect of differential reinforcement on the discrimination of visual number. *J. Psychol.*, *31*, 201–231.
- Mix, K. S., Levine, S. C., & Huttenlocher, J. (1997). Numerical abstraction in infants: Another look. *Dev. Psychol.*, *33*, 423–428.
- Moretto, G., & di Pellegrino, G. (2008). Grasping numbers. *Exp. Brain Res.*, *188*(4), 505–515.
- Naccache, L., & Dehaene, S. (2001). The priming method: Imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cereb. Cortex*, *11*(10), 966–974.
- Nieder, A. (2005). Counting on neurons: the neurobiology of numerical competence. *Nat. Rev. Neurosci.*, *6*(3), 177–190.
- Nieder, A., Diester, I., & Tudusciuc, O. (2006). Temporal and spatial enumeration processes in the primate parietal cortex. *Science*, *313*(5792), 1431–1435.
- Nieder, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science*, *297*(5587), 1708–1711.
- Nieder, A., & Merten, K. (2007). A labeled-line code for small and large numerosities in the monkey prefrontal cortex. *J. Neurosci.*, *27*(22), 5986–5993.
- Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude. Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron*, *37*(1), 149–157.
- Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proc. Natl. Acad. Sci. USA*, *101*(19), 7457–7462.
- Nunez, R. E., & Lakoff, G. (2000). *Where Mathematics Comes From: How the Embodied Mind Brings Mathematics into Being*. New York: Basic Books.
- Piaget, J. (1952). *The Child's Conception of Number*. New York: Norton.
- Piazza, M., Facoetti, A., Trussardi, A. N., et al. (2009). Developmental trajectories of number sense in normal and dyscalculic children. *submitted*.
- Piazza, M., Giacomini, E., Le Bihan, D., & Dehaene, S. (2003). Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging. *Proc. R. Soc. Lond. B Biol. Sci.*, *270*(1521), 1237–1245.
- Piazza, M., Izard, V., Pinel, P., et al. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, *44*(3), 547–555.
- Piazza, M., Mechelli, A., Price, C. J., et al. (2006). Exact and approximate judgements of visual and auditory numerosity: an fMRI study. *Brain Res.*, *1106*(1), 177–188.
- Piazza, M., Pinel, P., Le Bihan, D., et al. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron*, *53*, 293–305.
- Pica, P., Lemer, C., Izard, V., et al. (2004). Exact and approximate arithmetic in an Amazonian indigene group. *Science*, *306*(5695), 499–503.
- Pinel, P., Dehaene, S., Riviere, D., et al. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage*, *14*(5), 1013–1026.
- Pinel, P., Piazza, M., Le Bihan, D., et al. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron*, *41*(6), 983–993.
- Pinel, P., & Dehaene, S. (2009). Beyond hemispheric dominance: Brain regions underlying the joint lateralization of language and arithmetic to the left hemisphere. *J. Cogn. Neurosci.*, in press.
- Procyk, E., Tanaka, Y. L., & Joseph, J. P. (2000). Anterior cingulate activity during routine and non-routine sequential behaviors in macaques. *Nat. Neurosci.*, *3*(5), 502–508.
- Revsin, S., Piazza, M., Izard, V., et al. (2008). Does subitizing reflect numerical estimation? *Psychol. Sci.*, *19*(6), 607–614.
- Reynvoet, B., Brysbaert, M., & Fias, W. (2002). Semantic priming in number naming. *Quart. J. Exp. Psychol. A*, *55*(4), 1127–1139.
- Rips, L. J., Bloomfield, A., & Asmuth, J. (2008). From numerical concepts to concepts of number. *Behavioral and Brain Sciences*, *31*(6), 623–642.
- Rivera, S. M., Reiss, A. L., Eckert, M. A., et al. (2005). Developmental changes in mental arithmetic: Evidence for increased functional specialization in the left inferior parietal cortex. *Cereb. Cortex*, *15*(11), 1779–1790.

- Roggeman, C., Verguts, T., & Fias, W. (2007). Priming reveals differential coding of symbolic and non-symbolic quantities. *Cognition*, *105*(2), 380–394.
- Roitman, J. D., Brannon, E. M., & Platt, M. L. (2007). Monotonic coding of numerosity in macaque lateral intraparietal area. *PLoS Biol.*, *5*(8), e208.
- Roland, P. E., & Friberg, L. (1985). Localization of cortical areas activated by thinking. *J. Neurophysiol.*, *53*, 1219–1243.
- Sarnecka, B. W., & Gelman, S. A. (2004). Six does not just mean a lot: preschoolers see number words as specific. *Cognition*, *92*(3), 329–352.
- Sato, M., Cattaneo, L., Rizzolatti, G., et al. (2007). Numbers within our hands: modulation of corticospinal excitability of hand muscles during numerical judgment. *J. Cogn. Neurosci.*, *19*(4), 684–693.
- Sawamura, H., Shima, K., & Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey. *Nature*, *415*(6874), 918–922.
- Sereno, M. I., & Huang, R. S. (2006). A human parietal face area contains aligned head-centered visual and tactile maps. *Nat. Neurosci.*, *9*(10), 1337–1343.
- Shaki, S., & Fischer, M. H. (2008). Reading space into numbers – a cross-linguistic comparison of the SNARC effect. *Cognition*, *108*(2), 590–599.
- Shepard, R. N., Kilpatrick, D. W., & Cunningham, J. P. (1975). The internal representation of numbers. *Cog. Psychol.*, *7*, 82–138.
- Shuman, M., & Kanwisher, N. (2004). Numerical magnitude in the human parietal lobe; tests of representational generality and domain specificity. *Neuron*, *44*(3), 557–569.
- Siegler, R. S., & Booth, J. L. (2004). Development of numerical estimation in young children. *Child Dev.*, *75*(2), 428–444.
- Siegler, R. S., & Opfer, J. E. (2003). The development of numerical estimation: evidence for multiple representations of numerical quantity. *Psychol. Sci.*, *14*(3), 237–243.
- Sigman, M., & Dehaene, S. (2005). Parsing a cognitive task: a characterization of the mind's bottleneck. *PLoS Biol.*, *3*(2), e37.
- Sigman, M., & Dehaene, S. (2006). Dynamics of the central bottleneck: Dual-task and task uncertainty. *PLoS Biol.*, *4*(7), e220.
- Simon, O., Kherif, F., Flandin, G., Poline, J. B., Riviere, D., Mangin, J. F., et al. (2004). Automated clustering and functional geometry of human parietofrontal networks for language, space, and number. *NeuroImage*, *23*(3), 1192–1202.
- Simon, O., Mangin, J. F., Cohen, L., et al. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron*, *33*(3), 475–487.
- Simon, T. (1999). The foundations of numerical thinking in a brain without numbers. *Trends Cogn. Sci.*, *3*, 363–365.
- Smith, P. L., & Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends Neurosci.*, *27*(3), 161–168.
- Song, J. H., & Nakayama, K. (2008). Numeric comparison in a visually-guided manual reaching task. *Cognition*, *106*(2), 994–1003.
- Spelke, E. (2003). What makes us smart? Core knowledge and natural language. In D. Gentner & S. Goldin-Meadow (Eds.), *Language in Mind*. Cambridge, MA: MIT Press.
- Starkey, P., & Cooper, R. G. (1980). Perception of numbers by human infants. *Science*, *210*, 1033–1035.
- Tang, Y., Zhang, W., Chen, K., et al. (2006). Arithmetic processing in the brain shaped by cultures. *Proc. Natl. Acad. Sci. USA*, *103*(28), 10775–10780.
- Temple, E., & Posner, M. I. (1998). Brain mechanisms of quantity are similar in 5-year-olds and adults. *Proc. Natl. Acad. Sci. USA*, *95*, 7836–7841.
- Tomonaga, M., & Matsuzawa, T. (2002). Enumeration of briefly presented items by the chimpanzee (*Pan troglodytes*) and humans (*Homo sapiens*). *Anim. Learn. Behav.*, *30*(2), 143–157.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B., et al. (2006). A cortical region consisting entirely of face-selective cells. *Science*, *311*(5761), 670–674.
- Tudusciuc, O., & Nieder, A. (2007). Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proc. Natl. Acad. Sci. USA*, *104*(36), 14513–14518.
- Turconi, E., Campbell, J. L., & Seron, X. (2006). Numerical order and quantity processing in number comparison. *Cognition*, *98*(3), 273–285.
- Turconi, E., Jemel, B., Rossion, B., et al. (2004). Electrophysiological evidence for differential processing of numerical quantity and order in humans. *Brain Res. Cogn. Brain Res.*, *21*(1), 22–38.
- Turconi, E., & Seron, X. (2002). Dissociation between order and quantity meanings in a patient with Gerstmann syndrome. *Cortex*, *38*, 911–914.
- Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice: the leaky, competing accumulator model. *Psychol. Rev.*, *108*(3), 550–592.
- van Oeffelen, M. P., & Vos, P. G. (1982). A probabilistic model for the discrimination of visual number. *Percept. & Psychophysics*, *32*, 163–170.
- Venkatraman, V., Siong, S. C., Chee, M. W., V. (2006). Effect of language switching on arithmetic: a bilingual fMRI study. *J. Cogn. Neurosci.*, *18*(1), 64–74.
- Verguts, T., & Fias, W. (2004). Representation of number in animals and humans: a neural model. *J. Cogn. Neurosci.*, *16*(9), 1493–1504.

- Verguts, T., Fias, W., & Stevens, M. (2005). A model of exact small-number representation. *Psychon. Bull. Rev.*, *12*(1), 66–80.
- Viarouge, A., Hubbard, E., Dehaene, S., et al. Number line compression and the illusory perception of random numbers. submitted.
- Walsh, V. (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends Cogn. Sci.*, *7*(11), 483–488.
- Wynn, K. (1992a). Addition and subtraction by human infants. *Nature*, *358*, 749–750.
- Wynn, K. (1992b). Children's acquisition of the number words and the counting system. *Cog. Psychol.*, *24*, 220–251.
- Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition*, *74*(1), B1–B11.
- Zago, L., Petit, L., Turbelin, M. R., v (2008). How verbal and spatial manipulation networks contribute to calculation: An fMRI study. *Neuropsychologia*, *46*(9), 2403–2414.
- Zebian, S. (2005). Linkages between number concepts, spatial thinking, and directionality of writing: The SNARC effect and the REVERSE SNARC effect in English and Arabic monoliterates, biliterates, and illiterate Arabic speakers. *J. Cog. Culture*, *5*(1–2), 165–191.
- Zorzi, M., Priftis, K., & Umiltà, C. (2002). Brain damage: neglect disrupts the mental number line. *Nature*, *417*(6885), 138–139.